

CALCAREOUS FENS OF WESTERN NEW ENGLAND AND ADJACENT NEW YORK STATE

GLENN MOTZKIN

ABSTRACT

This study presents a community characterization of calcareous fens of western New England and adjacent New York State. Based on analyses of data from 24 sites, seven vegetation types are defined: *Carex lasiocarpa*-*Cladium mariscoides* Type, *Carex aquatilis* Type, *Betula pumila* Type, *Carex lacustris* Type, *Carex stricta* Type, *Typha angustifolia*-*Carex lasiocarpa* Type, and *Carex interior*-*Carex leptalea*-*Carex flava* Type. The distribution of these vegetation associations is related to hydrologic and ionic gradients. Calcareous fens of the region are similar to minerotrophically rich fens elsewhere in North America with respect to vegetation and environmental characteristics.

Key Words: wetlands, calcareous fens, vegetation classification, ordination

INTRODUCTION

Calcareous wetlands are ecologically significant communities that support numerous rare or uncommon plant species as well as several unusual animal species (McVaugh, 1957; Bernard et al., 1983; Rawinski and Rooney, 1989; Weatherbee, 1990). Historically limited in distribution and extent throughout the northeastern United States, modern development pressure continues to threaten the integrity of several sites.

Although calcareous wetlands are recognized as priorities for conservation, most previous investigations of freshwater wetlands in the northeastern United States have focused on peatlands characterized by acidic, nutrient-poor surface waters (Moizuk and Livingston, 1966; Hemond, 1980; Damman and French, 1987; among others). This research trend reflects the predominance of acidic bedrock throughout the region and has resulted in the general absence of information concerning the vegetation and environmental characteristics of circumneutral to alkaline wetlands. The present study marks the first comprehensive evaluation of calcareous fens in western New England and adjacent New York State, providing baseline information that is critical for conservation and management planning, as well as for future more detailed studies of these communities. The specific objectives of this study are to: 1) characterize vegetation associations of calcareous fens in western New England and adjacent New York

State, 2) relate variation in fen vegetation to environmental parameters, and 3) compare fens of the northeastern United States with those described from elsewhere in North America.

Calcareous fens are non-forested wetlands that are influenced by base-rich groundwater and contain calcicoles (Rawinski, 1984). In the present study, the term 'fen' is applied to both level and sloping communities with or without peat deposits. Although most studies of fens in North America have been restricted to peatlands (Schwintzer, 1978; Slack et al., 1980; Sims et al., 1982; Davis and Anderson, 1991), several European investigators have recognized the floristic and functional similarities between sites with peat and those that lack organic sediments (Wheeler, 1980; Boyer and Wheeler, 1989; Peterson, 1989).

STUDY AREA

In western New England and adjacent New York State, calcareous fens occur primarily as small communities (<1–50 ha) throughout the Berkshire Valley Lowland and portions of the adjacent Taconic Region where carbonate bedrock or surficial deposits occur (Figure 1). Many calcareous fens in the region occur on rocks of the Stockbridge formation, which consist primarily of marble, limestone, dolostone and other carbonate-rich rock types (Motts and O'Brien, 1981). A few fens overlie the Walloomsac and related formations that contain limestone interbedded with schists. A single fen in the Connecticut Valley of Massachusetts occurs on Mesozoic sedimentary bedrock. Although most fens occur on calcareous till deposits, several have developed on glaciofluvial or glaciolacustrine deposits.

Calcareous fens in the region occur at elevations that range from 75 to 400 m a.s.l., with most sites between 150–300 m. Climate throughout the region is continental, with cool winters and warm summers (U.S.D.A., 1988). Average annual precipitation of 110 cm is fairly evenly distributed throughout the year.

METHODS

The methods for this investigation are modified from those established for prior surveys for the Massachusetts Natural Her-

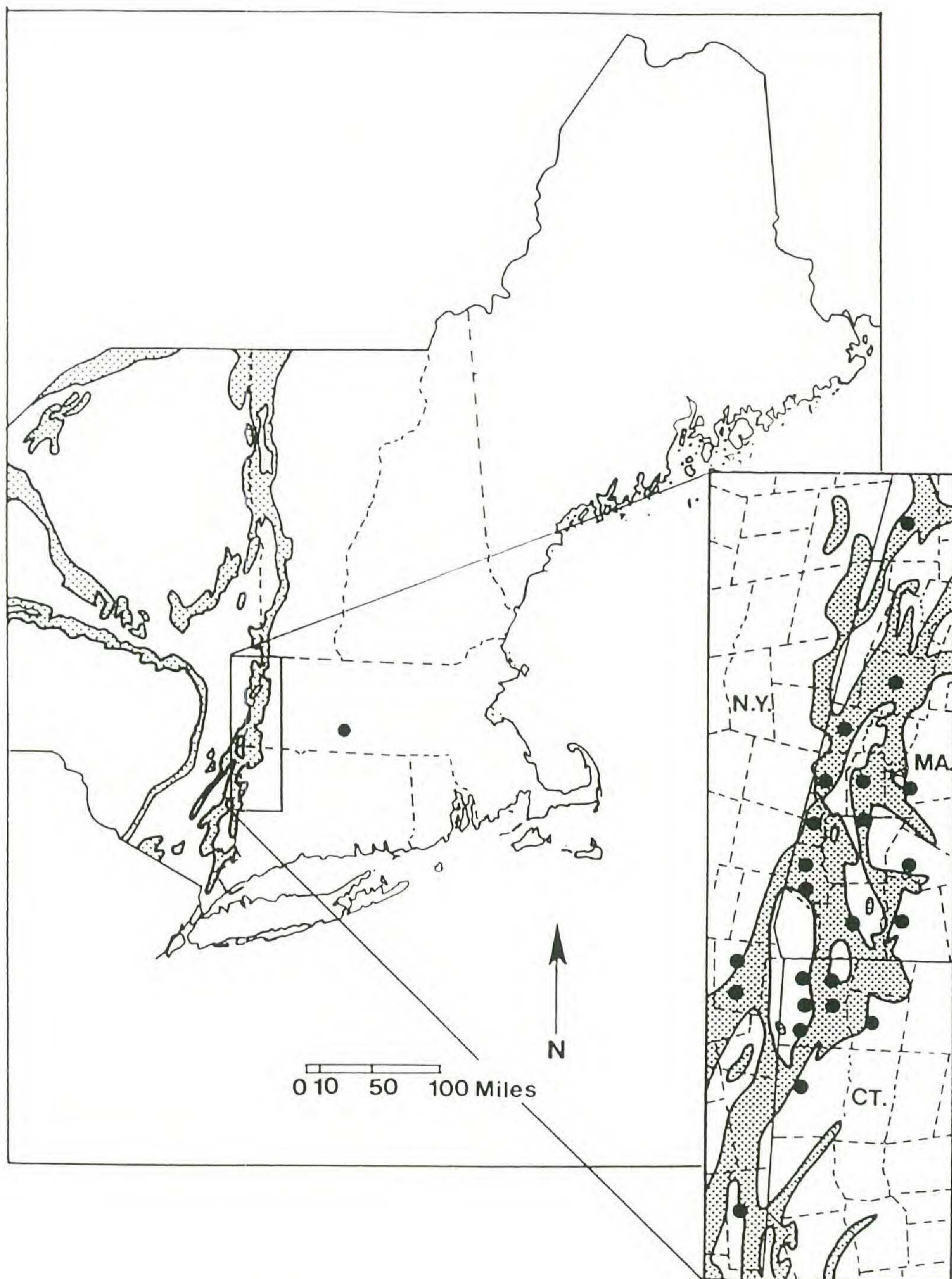


Figure 1. Map showing the location of the study area and the occurrence of carbonate bedrock (stippled) in the northeastern United States. Study sites are indicated as dots on the enlarged inset (right), except for one site in the Connecticut Valley that is indicated on the regional map (left). Modified from Moore (1935), Denny (1982), and Isachsen et al. (1991).

itage and Endangered Species Program (Motzkin, 1991). Field sites were selected in consultation with the staffs of the MA, CT, and NY Natural Heritage Programs and the Eastern Heritage Task Force of The Nature Conservancy. Twenty-four sites, believed to represent most of the undisturbed, non-forested fens in the region, were sampled for vegetation and environmental characteristics.

Fifty-five 100 m² relevés (Mueller-Dombois and Ellenberg, 1974) were sampled for vascular plant species-cover estimated within height strata and percent cover of dominant bryophytes. Relevés were subjectively located in areas of uniform vegetation and distributed to encompass a range of vegetation types. General observations of vegetation structure, landform type, site condition, disturbance history, and presence of rare species were also recorded. Bryophytes and unidentified herbaceous species were collected for identification. Nomenclature follows Seymour (1989) for vascular plants, except for *Carex* section *Stellulatae*, which follows Reznicek and Ball (1980), and *Carex stricta* complex, which follows Standley (1987). Nomenclature for bryophytes follows Crum (1976).

Surface water pH and conductivity were measured at each relevé location. Water samples were collected, refrigerated, and later analyzed at the University of Massachusetts using an atomic absorption spectrophotometer to determine concentrations of calcium, magnesium, and phosphorus. Water color of filtered samples (related to concentration of humic acids) was estimated in three classes: 'clear', 'moderate', or 'dark'. Depth of organic sediments at each relevé was determined by probing to a maximum depth of 2 m. A soil auger was used to determine the degree of decomposition of the upper one meter of organic sediments, estimated according to the Von Post scale (Clymo, 1983).

Relevé cover data were analyzed with cluster analysis and ordination techniques. Agglomerative cluster analysis (AGGLOM; Orloci, 1967) served as the basis for classifying vegetation types and detrended correspondence analysis (DCA; Hill, 1979) was useful in identifying relationships among relevés. Canonical correspondence analysis (CCA; ter Braak, 1986), correlation analysis, and Duncan's Multiple Range Tests were used to identify environmental factors influencing the distribution of plant communities.

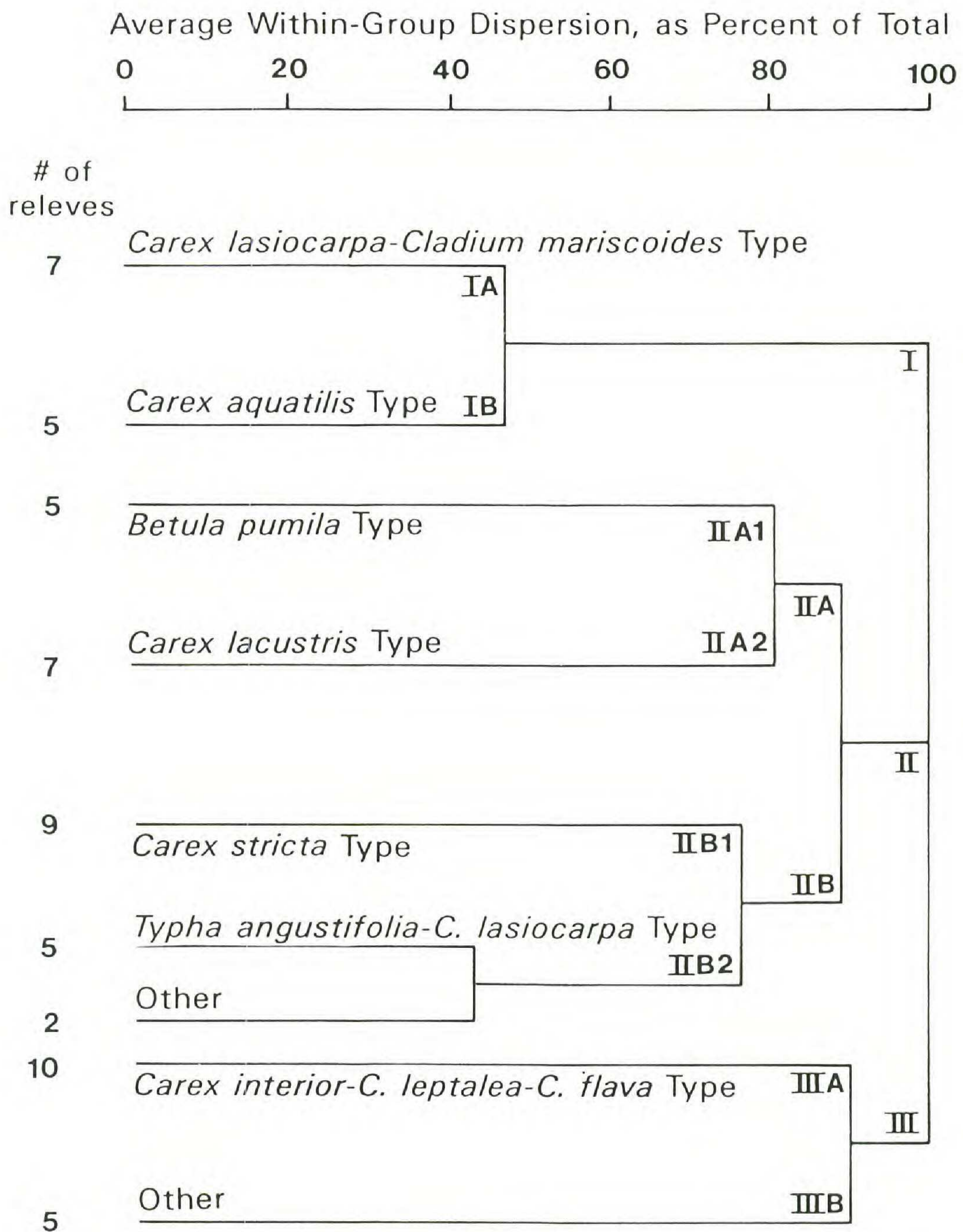


Figure 2. Simplified AGGLOM dendrogram based on absolute distances for species cover in 55 relevés. See text for description of vegetation types.

RESULTS

Vegetation Classification

Relevé data were clustered by AGGLOM using absolute distances into three main groups, composed of several smaller clus-

ters (Figure 2). Group I is characterized by *Carex lasiocarpa*, *C. aquatilis*, *Potentilla fruticosa*, and *Myrica gale*. *Cladium mariscoides*, *Rhynchospora alba*, *Sarracenia purpurea*, *Andromeda glaucophylla*, *Pogonia ophioglossoides*, *Drosera rotundifolia*, *Menyanthes trifolia*, and *Utricularia* spp. occur with greater frequency in this group than in Groups II or III (Table 1). *Sphagnum* spp. and *Campylium stellatum* are the common bryophytes. Uncommon species associated with Group I include *Carex limosa*, *C. aquatilis*, and others.

Group II is characterized by *Betula pumila*, *Carex lacustris*, *C. stricta*, *Thelypteris palustris*, *Salix candida*, other *Salix* species, and *Spiraea latifolia*. *Rhus vernix*, *Phragmites communis*, *Typha angustifolia*, *T. latifolia*, *Lythrum salicaria*, and *Lysimachia thyrsiflora* are also characteristic of this group. *Galium labradoricum*, *Betula pumila*, and *Salix candida* are species characteristic of Group II that are regionally uncommon.

Group III is characterized by *Carex interior*, *C. leptalea*, *C. flava*, *C. hystericina*, *Larix laricina*, *Parnassia glauca*, *Solidago patula*, *S. purshii*, and *Thelypteris palustris*, with *Rhamnus alnifolia*, *Equisetum fluviatile*, *Equisetum* spp., *Ribes* spp., and *Cornus* spp. also important. Rare species include *Carex sterilis*, *C. tetanica*, *Equisetum scirpoides*, *Petasites palmatus*, *Lobelia kalmii*, and *Spiranthes romanzoffiana*.

Within the classification hierarchy, subgroups are characterized by a subset of the species listed for the major groups as well as by additional species. Subgroups that are distinct with respect to species composition and abundance may be considered separate vegetation types (Table 1). Group I includes two such subgroups. The ***Carex lasiocarpa*-*Cladium mariscoides* Type** (Subgroup IA) is a sedge-dominated association characterized by *Carex lasiocarpa*, *Myrica gale*, *Potentilla fruticosa*, *Peltandra virginica*, and *Cladium mariscoides*. Other frequent species include *Drosera rotundifolia*, *Sarracenia purpurea*, *Hypericum virginicum*, *Rhynchospora alba*, *Typha* species, *Vaccinium macrocarpon*, and *Utricularia* spp. The dominant bryophytes are *Campylium stellatum*, *Calliergonella* sp., and *Sphagnum* spp.

The ***Carex aquatilis* Type** (Subgroup IB) is structurally similar to Subgroup IA but is dominated by *Carex aquatilis* or by *Carex aquatilis* and *C. lasiocarpa* and lacks species such as *Peltandra virginica* and *Hypericum virginicum*.

Group II includes four subgroups. The ***Betula pumila* Type** (Subgroup IIA1) is characterized by a shrub layer of *Betula pumi-*

Table 1. Percent frequency of occurrence by Group and Subgroup. * = incomplete sampling of minor bryophytes; no frequencies calculated.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Trees							
<i>Chamaecyparis thyoides</i>	14						
<i>Acer rubrum</i>	14	20	100	14	57	40	40
<i>Fraxinus</i> spp.			20		29		20
<i>Pinus strobus</i>					14		70
<i>Larix laricina</i>			20				40
<i>Tsuga canadensis</i>							30
<i>Betula alleghaniensis</i>					14		20
<i>Carpinus caroliniana</i>					14		20
<i>Populus tremuloides</i>							20
<i>Quercus alba</i>							20
<i>Betula papyrifera</i>							10
<i>Tilia americana</i>							10
Shrubs							
<i>Chamaedaphne calyculata</i>	14						
<i>Lonicera villosa</i>	14						
<i>Aronia arbutifolia</i>	14					20	10
<i>Andromeda glaucophylla</i>	14	40					
<i>Myrica gale</i>	86	100	40		14	40	
<i>Potentilla fruticosa</i>	86	100	100	71	43	20	80
<i>Alnus</i> spp.	43	40	40	14	86	60	20
<i>Salix discolor</i>	14	20	40	71	14		40
<i>Spiraea latifolia</i>	14		40	43	71	60	40
<i>Cornus stolonifera</i>	14		80	14		40	50
<i>Cephalanthus occidentalis</i>	14		20	14	14	60	
<i>Salix candida</i>		20	20	57	14	80	10
<i>Betula pumila</i>		60	100			40	
<i>Rhus vernix</i>			40	14	14	20	20
<i>Rhamnus alnifolia</i>			20	14			40
<i>Ribes</i> spp.			20	14			60
<i>Salix serissima</i>			40	43	14		50
<i>Salix</i> spp.			60	14	43	20	60
<i>Rosa palustris</i>			40		29		10
<i>Viburnum recognitum</i>			20		14	20	10
<i>Rhamnus frangula</i>			20				
<i>Ilex verticillata</i>			20				
<i>Myrica pensylvanica</i>			20				
<i>Cornus amomum</i>				29	14		
<i>Cornus racemosa</i>				14	14		20
<i>Spiraea tomentosa</i>					14		10
<i>Lyonia ligustrina</i>					14		40
<i>Lindera benzoin</i>					14		20
<i>Amelanchier</i> sp.					14		20

Table 1. Continued.

Group: Subgroup:	I		II				III
	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
<i>Vaccinium corymbosum</i>						20	10
<i>Viburnum lentago</i>							30
<i>Corylus</i> spp.							10
<i>Ulmus</i> sp.							10
<i>Vaccinium angustifolium</i>							10
<i>Hamamelis virginiana</i>							10
<i>Rhamnus cathartica</i>							10
Graminoids							
<i>Rhynchospora alba</i>	43						10
<i>Eriophorum gracile</i>	14						
<i>Scirpus acutus</i>	43	20		14		20	
<i>Scirpus hudsonianus</i>	14	40					
<i>Cladium mariscoides</i>	86	60					
<i>Carex lasiocarpa</i>	100	60			14	100	
<i>Carex aquatilis</i>	14	100	40			20	
<i>Phragmites communis</i>		20	40			40	
<i>Carex limosa</i>		20					
<i>Carex prairea</i>		20	40	14	14	40	10
<i>Calamagrostis canadensis</i>			60	57	29	20	10
<i>Poa palustris</i>	14		20				
<i>Carex lacustris</i>			80	100		40	10
<i>Eleocharis erythropoda</i>		20	20	43			20
<i>Carex stricta</i>			40	57	100	60	20
<i>Carex stipata</i>					57		
<i>Scirpus atrovirens</i>					43		30
<i>Carex vulpinoidea</i>					29		
<i>Dulichium arundinaceum</i>						60	
<i>Eleocharis</i> sp.	29	40			14	60	30
<i>Carex comosa</i>			20	14	14	20	
<i>Carex interior</i>			60	29	14		100
<i>Carex leptalea</i>			40	29			100
<i>Carex flava</i>		20	40		29	40	90
<i>Carex hystericina</i>				29	43		80
<i>Carex tetanica</i>			20				30
<i>Eriophorum viridi-carinatum</i>	14				14		50
<i>Glyceria striata</i>			20	43		20	50
<i>Juncus</i> sp.				14	14	20	20
<i>Muhlenbergia glomerata</i>	14		20	14	14		50
<i>Carex scoparia</i>				14	14		
<i>Phalaris arundinacea</i>				14			
<i>Bromus ciliatus</i>			20		14		30
<i>Juncus dudleyi</i>					14		30
<i>Juncus effusus</i>					14		20

Table 1. Continued.

Group: Subgroup:	I		II				III
	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
<i>Juncus nodosus</i>					14		50
<i>Eleocharis acicularis</i>					14		
<i>Leersia oryzoides</i>					14		
<i>Carex rostrata</i>					14		
<i>Poa pratensis</i>					29		10
<i>Carex granularis</i>							40
<i>Anthoxanthum odoratum</i>							20
<i>Festuca</i> spp.							20
<i>Poa compressa</i>							10
<i>Sphenopholis</i> sp.							10
<i>Carex gracillima</i>							10
<i>Carex laevivaginata</i>							10
<i>Carex</i> spp.	14						10
<i>Andropogon scoparius</i>							10
<i>Danthonia spicata</i>							10
Herbs							
<i>Utricularia</i> spp.	29						
<i>Potamogeton</i> spp.	29						
<i>Potentilla palustris</i>	29		40				
<i>Peltandra virginica</i>	71		40		14	40	
<i>Pogonia ophioglossoides</i>	29	20					10
<i>Drosera rotundifolia</i>	86	20				20	50
<i>Sarracenia purpurea</i>	100	80					
<i>Vaccinium macrocarpon</i>	100	80	20				
<i>Menyanthes trifolia</i>	86	100	20			20	
<i>Utricularia intermedia</i>	57	80	20		14		
<i>Typha latifolia</i>	14	60	60	57	14		10
<i>Equisetum fluviatile</i>			100	43	14	40	
<i>Lysimachia thyrsiflora</i>			100	14		40	10
<i>Osmunda regalis</i>	14		40	14			10
<i>Sagittaria latifolia</i>			40		14	20	
<i>Parthenocissus quinquefolia</i>			20		14		
<i>Rubus</i> spp.			80	29	29		40
<i>Polygonum</i> sp.			20	29	29		
<i>Acorus calamus</i>				29			10
<i>Lemnaceae</i> spp.				14	14		
<i>Galium labradoricum</i>			40	43	14		10
<i>Iris versicolor</i>			40	57	14	40	20
<i>Impatiens capensis</i>			20	14	43		
<i>Viola</i> sp.			20		19		
<i>Brasenia schreberi</i>					29		
<i>Solidago</i> spp.			40		14		20
<i>Typha angustifolia</i>	43		40	14	29	100	

Table 1. Continued.

Group: Subgroup:	I		II				III
	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
<i>Thelypteris palustris</i>	29		100	86	71	100	90
<i>Hypericum virginicum</i>	71		20	14	57	80	
<i>Lythrum salicaria</i>			60	14	29	60	20
<i>Eupatorium maculatum</i>			40	43	43		40
<i>Onoclea sensibilis</i>			20	14	29	20	20
<i>Eupatorium perfoliatum</i>				14	14	20	20
<i>Aesclepias incarnata</i>			20	29		40	
<i>Proserpinaca palustris</i>			20	14		20	
<i>Campanula aparinoides</i>					29	40	
<i>Solidago patula</i>					43	20	90
<i>Utricularia minor</i>			20				
<i>Equisetum</i> spp.				14	14		80
<i>Parnassia glauca</i>				43			80
<i>Solidago purshii</i>	14	20	20	43			70
<i>Symplocarpus foetidus</i>			40	43	14	20	50
<i>Thalictrum polygamum</i>			40	14			40
<i>Solanum dulcamara</i>			20	14			
<i>Galium</i> spp.				29	43		40
<i>Rumex</i> spp.				29	14		
<i>Ludwigia palustris</i>				14	14		
<i>Verbena hastata</i>				14			
<i>Umbelliferae</i> spp.				29			10
<i>Hydrocotyl americana</i>					14		40
<i>Achillea millefolium</i>					14		20
<i>Compositae</i> spp.					29		20
<i>Lonicera</i> spp.					14		20
<i>Lysimachia ciliata</i>					14		10
<i>Apios americana</i>					14		10
<i>Nuphar variegatum</i>					14		
<i>Boehmeria cylindrica</i>					14		
<i>Desmodium</i> sp.					14		
<i>Geum rivale</i>							40
<i>Senecio aureus</i>							40
<i>Prunella vulgaris</i>							30
<i>Petasites palmatus</i>							20
<i>Smilacina stellata</i>							20
<i>Potentilla simplex</i>							20
<i>Fragaria</i> sp.							20
<i>Eupatorium rugosum</i>							10
<i>Tussilago farfara</i>							10
<i>Amphicarpa bracteata</i>							10
<i>Geranium maculatum</i>							10
<i>Houstonia</i> sp.							10
<i>Cardamine</i> sp.							10

Table 1. Continued.

Group: Subgroup:	I		II				III
	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
<i>Sanicula marilandica</i>							10
<i>Spiranthes romanzoffiana</i>							10
<i>Taraxacum officinale</i>							10
<i>Chrysanthemum leucanthemum</i>							10
<i>Clematis</i> spp.							10
<i>Cypripedium reginae</i>							10
<i>Adiantum pedatum</i>							10
<i>Aster puniceus</i>							10
<i>Aster schreberi</i>							10
<i>Aster umbellatus</i>							10
<i>Dryopteris cristata</i>							10
<i>Epilobium leptophyllum</i>	14						10
<i>Equisetum scirpoides</i>							10
<i>Lycopus uniflora</i>							10
<i>Lysimachia terrestris</i>						20	10
<i>Mentha arvensis</i>							
Unknown	14		20	14	29		20
Bryophytes							
<i>Sphagnum fimbriatum</i>	14						
<i>Sphagnum subsecundum</i>	14						
<i>var. contortum</i>							
<i>Drepanocladus</i> sp.	14		20	14		60	
<i>Calliergonella</i> sp.	71	40	60	14	14	40	10
<i>Campylium stellatum</i>	86	100	80	57	29	40	60
<i>Sphagnum warnstorffii</i>	14						30
<i>Sphagnum</i> spp.							20
<i>Sphagnum magellanicum</i>							10
<i>Thuidium delicatulum</i>			*				
<i>Leptodictyum</i> sp.					*		
<i>Aulacomnium palustre</i>							*
<i>Cratoneuron filicinum</i>							*
<i>Scorpidium scorpioides</i>							*
<i>Tomenthypnum nitens</i>							*
<i>Helodium blandowii</i>							*
<i>Dicranum scoparium</i>							*
<i>Thuidium recognitum</i>							*

la, *Potentilla fruticosa*, *Acer rubrum*, *Cornus stolonifera*, and *Salix* spp., amidst herbaceous species such as *Carex lacustris*, *Calamagrostis canadensis*, *Typha angustifolia*, *T. latifolia*, *Lysimachia thyrsiflora*, *Lythrum salicaria*, *Thelypteris palustris*, *Equisetum*

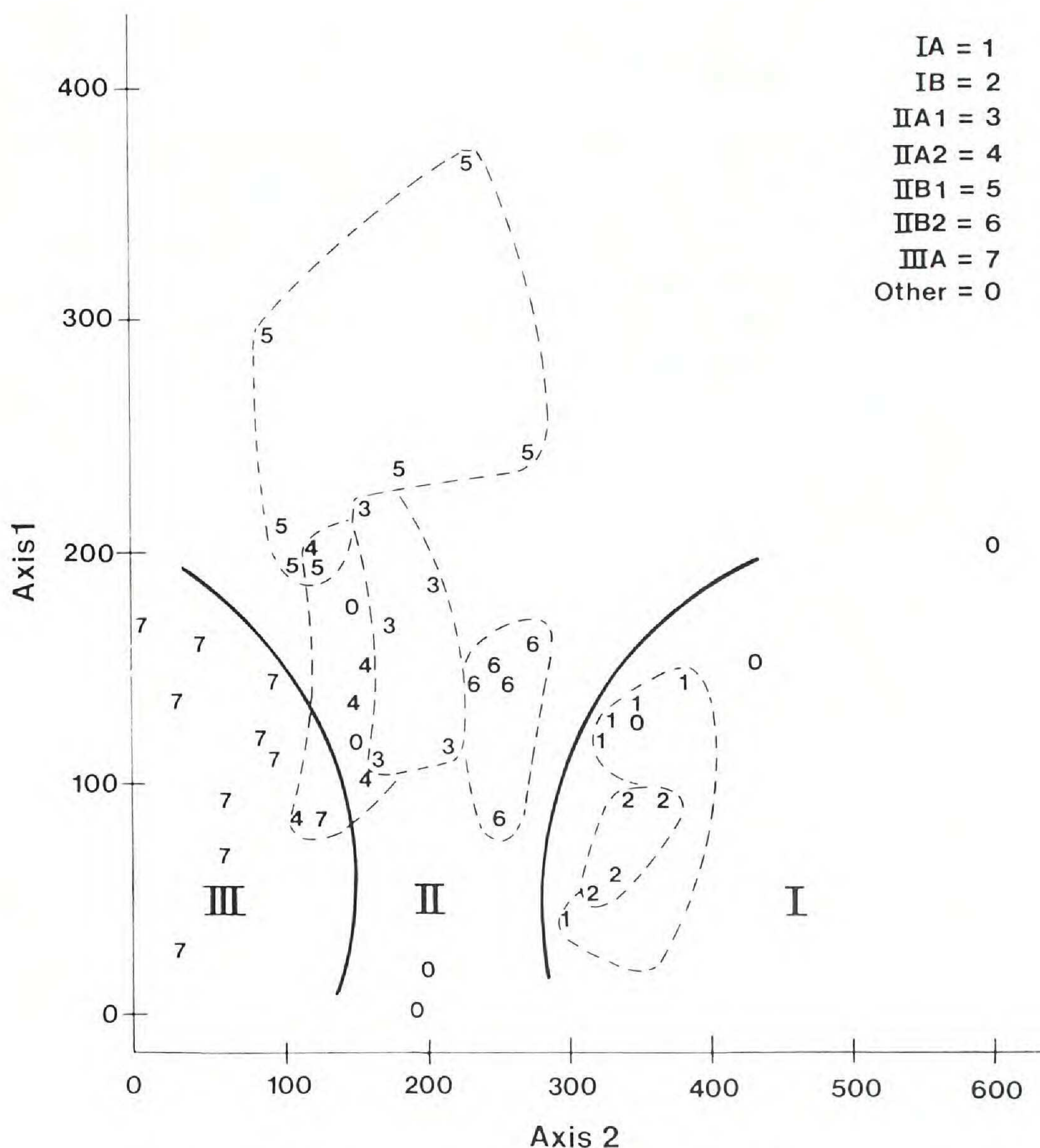


Figure 3. Plot of DCA sample ordination for axes 1 and 2. Numbers refer to groups and subgroups defined by cluster analysis (Figure 2).

fluviatile, and *Campyllum stellatum*. *Rhus vernix* is locally abundant.

The ***Carex lacustris* Type** (Subgroup IIA2) includes some of the species found in the *Betula pumila* type, but lacks extensive woody cover. Frequent species include *Carex lacustris*, *C. stricta*, *Salix candida*, *Potentilla fruticosa*, *Typha* spp., and *Thelypteris palustris*.

The ***Carex stricta* Type** (Subgroup IIB1) has higher frequency and cover values for *Carex stricta* than other subgroups. *Acer*

rubrum, *Alnus* sp., *Scirpus atrovirens*, *Galium* spp., *Eupatorium maculatum*, and *Thelypteris palustris* are other characteristic species.

The ***Typha angustifolia*-*Carex lasiocarpa* Type** (Subgroup IIB2) is dominated by *Typha angustifolia* and *Carex lasiocarpa*, with *Salix candida*, *Cephalanthus occidentalis*, *Dulichium arundinaceum*, *Eleocharis* spp., *Campanula aparinoides*, and *Hypericum virginicum* frequently encountered. *Potentilla fruticosa* is less frequent in this subgroup than in any other vegetation type identified through cluster analysis. Two plots in this Subgroup are shown as 'Other' in Figure 2. These plots are dominated by *Scirpus acutus* with only low cover of species characteristic of the *Typha angustifolia*-*Carex lasiocarpa* Type.

Group III includes two subgroups. The ***Carex interior*-*C. leptalea*-*C. flava* Type** (Subgroup IIIA) has sparse tree and shrub strata containing *Pinus strobus*, *Larix laricina*, *Potentilla fruticosa*, *Salix serissima*, *Ribes* spp., and *Rhamnus alnifolia*, and a low herbaceous stratum characterized by *Carex interior*, *C. leptalea*, *C. flava*, *C. hystericina*, *Juncus dudleyi*, *J. nodosus*, *Muhlenbergia glomerata*, *Parnassia glauca*, *Solidago purshii*, and *S. patula*. Relevés in Subgroup IIIB are shown as 'Other' in Figure 2 because these plots contain vegetation that appears transitional between two or more of the types described above.

Figure 3 presents the results of the DCA ordination, with relevés assigned according to the groups and subgroups defined by cluster analysis. The grouping of relevés along the ordination axes demonstrates the lack of overlap between types defined by cluster analysis at both a coarse (major groups) and fine level (subgroups) of classification.

Environmental Characteristics

The surface waters of the calcareous fens investigated are circumneutral to alkaline (pH: 6.0–8.1), with relatively high concentrations of calcium (8–65 mg/liter) and magnesium (4–32 mg/liter) (Table 2). Phosphorus levels are low, with only 8 out of 55 samples above the detection limit of .15 ppm (not shown in Table 2). Depth of organic sediments range from >200 cm in most Group I sites to 0–15 cm in areas with visible groundwater seepage (Group III). Where organic sediments occur, the degree of de-

Table 2. Environmental characteristics of calcareous fens of western New England and adjacent New York State (average value with range in parentheses). Groups and vegetation types numbered as in Figure 3. Color refers to filtered samples (1 = clear, 2 = moderate, 3 = dark).

	No. of Samples	pH	Conductivity (μ mho)	CA (mg/liter)	MG (mg/liter)	Depth* (cm)	Von Post (0–10)	Color (1–3)
Group I	12	6.6 (6.0–7.1)	415 (87–1151)	31 (11–62)	10 (4–17)	200	3 (2–3)	2 (1–3)
Type 1	7	6.5 (6.0–7.0)	213 (87–322)	22 (11–34)	10 (4–17)	200	3 (3–3)	2 (1–3)
Type 2	5	6.8 (6.5–7.1)	697 (225–1151)	43 (26–62)	10 (7–14)	200	3 (2–3)	2 (1–3)
Group II	26	6.9 (6.5–7.7)	366 (208–581)	43 (8–65)	19 (7–32)	135 (20–200)	7 (3–9)	2 (1–3)
Type 3	5	6.8 (6.7–6.8)	391 (251–505)	43 (34–52)	19 (11–26)	171 (55–200)	5 (3–8)	2 (1–2)
Type 4	7	6.8 (6.5–7.4)	341 (225–461)	50 (30–62)	16 (10–22)	141 (65–200)	7 (3–9)	1 (1–3)
Type 5	9	7.1 (6.7–7.7)	371 (248–515)	45 (16–65)	19 (7–32)	103 (20–200)	8 (3–9)	2 (1–3)
Type 6	5	6.9 (6.7–7.2)	368 (208–581)	35 (8–50)	22 (15–29)	150 (75–200)	5 (3–9)	1 (1–2)
Group III	10	7.2 (6.9–8.1)	333 (158–478)	46 (26–62)	17 (8–23)	20 (0–70)	7 (3–9)	1 (1–2)
Type 7	10	7.2 (6.9–8.1)	333 (158–478)	46 (26–62)	17 (8–23)	20 (0–70)	7 (3–9)	1 (1–2)

* Maximum value of 200 cm.

composition within the uppermost one meter of sediments varies from largely undecomposed peat (Von Post scale: 2–3) in many Group I plots, to highly decomposed muck (Von Post: 7–9) in Group II sites.

Correlation analyses indicate a significant negative relationship between depth of organic sediments and pH ($R = -.63$; $P = .0001$), degree of decomposition ($R = -.45$; $P = .0017$), and Mg concentration ($R = -.33$; $P = .02$). Ca concentration is positively correlated with Mg concentration ($R = .58$; $P = .0001$), and with conductivity ($R = .49$; $P = .0004$), and both Ca and Mg are negatively correlated with hydrogen ion concentration (Ca: $R = -.39$, $P = .01$; Mg: $R = -.39$, $P = .01$). pH is positively correlated with degree of decomposition of peat ($R = .34$; $P = .03$). Water color is positively correlated with hydrogen ion concentration ($R = .36$; $P = .01$).

Relationship Between Vegetation and Environment

Canonical correspondence analysis (CCA; ter Braak, 1986), a form of direct gradient analysis in which the vegetation ordination is constrained by environmental data, was used to relate vegetation variability to measured environmental variables. In the resulting ordination (Figure 4), relevés separate primarily along gradients of depth of organic sediments, pH, and degree of decomposition of organics. Ca, Mg, conductivity, and water color account for less of the variability in the vegetation. Combined, these environmental factors account for a relatively low percentage of the total variability of the vegetation ($\sim 25\%$), reflecting the fact that the fens investigated are highly variable with respect to vegetation and water chemistry. ter Braak (1986) has noted this pattern for other data sets, suggesting that CCA may still be useful in cases where a relatively low percentage of the total variability is accounted for by the ordination diagram.

The hierarchical nature of cluster analysis allows one to test the hypothesis that different environmental variables are associated with vegetation variation at different levels of classification. For example, in montane systems one might hypothesize that elevation gradients are responsible for patterns of vegetation variation at a coarse level. Within a particular elevation zone, however, local edaphic factors (rather than elevation) might control patterns of vegetation variation. Duncan's Multiple Range Tests

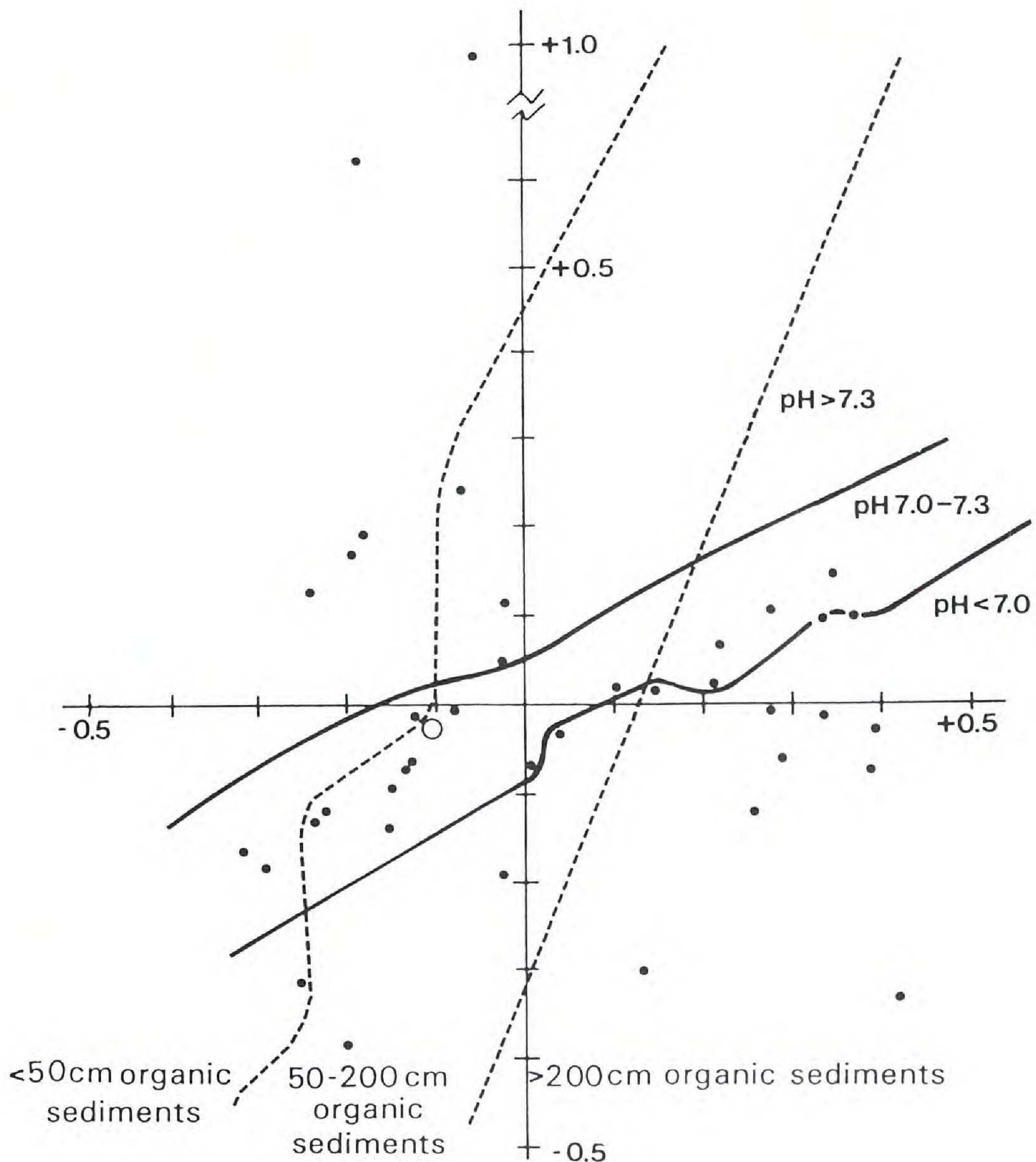


Figure 4. Plot of CCA sample ordination for axes 1 and 2. Broken lines distinguish plots with >200 cm, 50–200 cm, and <50 cm of organic sediments. Solid wavy lines separate plots with pH values of >7.3 , 7.0–7.3, and <7.0 . An outlier with respect to pH class (pH = 7.4) is indicated by an open circle.

were used to determine which environmental factors differ significantly with respect to major vegetation groups and subgroups defined by cluster analysis.

At the coarse level of classification, depth to mineral soil is the only variable measured that differs significantly ($P = .0001$) between all three groups. Hydrogen ion concentration, Mg, and degree of decomposition of organics (Von Post value) for Group

I are significantly different ($P = .01$, $P = .0004$ and $P = .0001$, respectively) from Groups II and III (which are not different from each other). Calcium levels are different ($P = .07$) between Groups I and III, but not between Groups I and II or between Groups II and III. Conductivity and color of filtered samples do not vary significantly among the three groups. These results suggest that Groups I and III (defined by cluster analysis of relevé data) are most different with respect to environmental parameters (e.g., depth of sediments, pH, Mg, degree of decomposition, and Ca) and that Group II is intermediate with respect to these variables. As with the CCA results, depth to mineral soil is the single variable most strongly associated with vegetation patterns at this level of classification.

Similar analyses were performed to determine environmental differences between subgroups within each major cluster group. Within Group I, Subgroup 1A differs significantly from Subgroup 1B with respect to Ca concentration ($P = .0223$) and conductivity ($P = .0098$). Within Group II, only Von Post values differ between the subgroups ($P = .0767$), with Subgroup IIB1 significantly different from Subgroup IIA1 (but not from IIA2 and IIB2), and Subgroups IIA1, IIA2, and IIB2 not significantly different from each other. No other environmental parameters tested differ significantly between subgroups defined by cluster analysis. Group III contains only one subgroup (IIIA) considered to be a distinct vegetation type, and so was not included in this level of analysis.

DISCUSSION

Relationship of Vegetation to other North American Fens

The coarse level of classification determined through cluster analysis of relevé data can be related to existing classifications of calcareous wetlands. Group I corresponds to a Lake Basin Graminoid Fen type described from the Northeast (Rawinski, 1984; Weatherbee, 1990), and to a Rich Graminoid Fen type of New York State (Reschke, 1990). Dominant species in this group are also recorded from minerotrophic fens of northern Michigan (Schwintzer, 1978). Group II contains elements of the Seepage Swamps of highly calcareous soils described by McVaugh (1957)

and the Seepage Marsh of Rawinski (1984), which he describes as having characteristics of both fen and marsh. Rich-fen types from Britain are structurally similar to Group II vegetation (Wheeler, 1980). Group III, which corresponds to Reschke's (1990) Rich Sloping Fen and to Rawinski's (1984) Calcareous Sloping Fen, contains several species considered to be 'rich fen indicator species' in Ontario (e.g., *Carex leptalea*, *Eriophorum viridi-carinatum*, *Scorpidium scorpioides*; Sims et al., 1982).

Several of the vegetation types (subgroups) described here are also related to types found elsewhere in North America. The *Carex lasiocarpa*-*Cladium mariscoides* Type (Subgroup IA) has been described from a Maine peatland (Rawinski and Rooney, 1989). The vascular vegetation of the *Carex aquatilis* Type is apparently related to the *Drepanocladus revolvens*-*Carex aquatilis* association found in patterned rich fens in western Alberta (Slack et al., 1980), although none of the study sites investigated in our region display the physiographic patterning typical of fens in boreal climates (Foster and King, 1984; Glaser, 1987). Additional work is needed to evaluate the bryophyte composition of this type.

The *Betula pumila* Type corresponds to a 'larch-birch-sumac swamp type' described from a site included in this investigation (McVaugh, 1957) and to the Rich Shrub Fens of New York (Reschke, 1990). The *Carex stricta* Type is apparently similar to the Sedge Meadow communities found in Maine and New York (Reschke, 1990; Gawler, 1991). No published descriptions correspond closely to the *Typha angustifolia*-*Carex lasiocarpa* Type.

The *Carex interior*-*C. leptalea*-*C. flava* Type contains species described by numerous authors as typical of rich calcareous fens (e.g., Sims et al., 1982; Vitt and Chee, 1990), although no specific reference to this association occurs from outside the region.

Field observations suggest that two additional vegetation associations occur in fens of the region but were inadequately sampled in the current study. A *Scirpus acutus* association was observed in several of the largest peatland fens and along marl pond shores. Also, extensive *Phragmites communis*-dominated areas occur in association with several of the vegetation types described above. Additional sampling is required to relate these associations to the vegetation classification presented here and to those developed for other regions of North America.

Environmental Characteristics

Several authors have related vegetation patterns to environmental characteristics of graminoid-dominated peatland fens elsewhere in North America (Schwintzer, 1978; Slack et al., 1980; Sims et al., 1982; Foster and King, 1984; Vitt and Chee, 1990). Comparison of environmental characteristics reported here (Table 2) with those of previous investigations (Table 3) suggests that the groups and subgroups defined in the current study are comparable to minerotrophically rich fens sampled throughout North America. Of the types considered here, Group I is apparently the least 'rich' (with respect to surface water chemistry), Group II sites are intermediate, and Group III may be characterized as extremely rich (Table 2).

Group I represents a peatland-fen type characterized by deep organic sediments, permanently saturated conditions, and consolidated or floating, sedge-dominated organic mats. Although little is known of the developmental history of these fens in our region, preliminary observations of the macrofossil stratigraphy of two sediment cores extracted from Kampoosa Fen in Stockbridge, MA indicate that since the development of a peat mat at this site, fairly uniform sedge and shrub-sedge peat has accumulated to a depth of 270 cm. This suggests that vegetation structurally similar to the modern vegetation has occupied the site since the time of peat mat establishment. Although the time it has taken for these 270 cm of sediments to accumulate is not known, an estimate of a few thousand years seems reasonable, based on estimates of peat accumulation rates from throughout northeastern North America. Thus, the vegetation at this site appears relatively stable and there is no indication of rapid infilling or terrestrialization.

Sites supporting Group II vegetation are characterized by 50–200+ cm of moderate to well-decomposed organic sediments occurring in a variety of seasonally inundated depressions and drainages. Vegetation characteristic of this group occurs in basins that also support Group I vegetation, in canopy gaps within rich forested swamps, in drainages with current or former beaver impoundments, and in level to slightly sloping sites adjacent to Group III vegetation.

Group III sites are slightly to moderately sloping with groundwater seepage frequently visible in distinct rivulets. In areas of

Table 3. Chemical properties of waters from North American wetlands (average values with range in parentheses). From Zoltai (1988).

Wetland Class	No. of Samples	pH	Conductivity (μ mho)	CA (mg/liter)	MG (mg/liter)	Source
Bog	18	4.0 (3.7–4.4)	—	2.3 (1.2–3.7)	0.4 (0.2–0.9)	Schwintzer (1981)
	13	(4.6–5.1)	(35–62)	(0.2–0.8)	(0.1–0.2)	Gauthier (1980)
	10	(3.8–4.4)	31	0.2	0.1	Foster and King (1984)
Fen (poor)	193	(4.6–5.2)	(18–59)	(0.4–4.8)	(0.1–0.7)	Gauthier (1980)
	14	(4.7–5.5)	49	0.3	0.2	Foster and King (1984)
	1	5.0	—	2.4	0.4	Vitt et al. (1975)
Fen (moderately poor)	42	5.2	65	1.1	0.2	Gauthier (1980)
Fen (intermediate to rich)	9	7.2 (6.8–7.9)	281 (140–456)	28 (18–37)	11 (4–28)	Slack et al. (1980)
	21	6.1 (5.2–6.9)	59 (33–128)	10 (4–18)	—	Glaser et al. (1981)
	5	6.5 (5.4–7.1)	—	43 (7–124)	10 (2–15)	Schwintzer (1978)
Swamp (coniferous)	12	7.2 (6.9–7.8)	—	40 (22–52)	12 (8–17)	Schwintzer (1981)

heavy groundwater discharge, mineral soil is typically exposed. Elsewhere, small hummocks develop with shallow accumulations of organic matter. Field observations suggest that the importance of woody species in seepage fens is inversely related to disturbance, with more highly disturbed sites (i.e., those that are flooded by beavers, grazed, or mowed) supporting only low, scattered shrubs. A similar pattern has been described from European fens (Regnéll, 1980; Peterson, 1989).

Environmental Gradients and Vegetation Distribution

CCA analyses indicate that depth to mineral soil is the environmental parameter that accounts for the greatest portion of the variability in the relevé data, with degree of decomposition of organics and pH also important. Duncan's Multiple Range Tests also indicate depth as a significant variable, along with degree of decomposition, pH, Ca, and Mg concentrations. In the study sites considered, depth of peat probably reflects a gradient of 'rate of groundwater-flow' ranging from 'slow' (and poorly aerated) in well-defined basins with deep peat accumulations (Group I), to relatively 'rapid' (and well aerated) in sloping (Group III) sites that lack peat. Depth of peat may also indicate the relative availability to vegetation of nutrients or cations derived from contact with mineral soil. The results of both CCA and Duncan's Multiple Range Tests suggest the importance of both hydrologic gradients (as indicated by depth of organic sediments) and ionic gradients related to alkalinity-acidity (pH, Mg, and Ca concentrations) in determining the variability between the rich fen types considered here.

Similar hydrologic and ionic gradients have been related to vegetation distribution in fen types throughout North America. Peat depth, pH, water levels, and water chemistry are related to differences between fens in Canada (Slack et al., 1980; Sims et al., 1982; Vitt and Chee, 1990). Vegetation variation in a peat and marl fen in western New York is related to complex gradients associated with hydrology, soil organic matter, and soil carbonate-carbon concentrations (Bernard et al., 1983). In one of the few detailed studies to consider non-peatland fens, Boyer and Wheeler (1989) suggest that structural and compositional variation in seepage fens in Britain is related to differences in phosphorus availability between high and low groundwater discharge areas.

At a fine level of classification, subgroups within Group II do not differ significantly with respect to most environmental parameters measured. This probably reflects the high degree of variability of the measured environmental parameters, a pattern noted by several authors (e.g., Sims et al., 1982) for rich fens elsewhere in North America.

Within Group I, relevés in the *Carex lasiocarpa*-*Cladium mariscoides* Type differ significantly from those in the *Carex aquatilis* Type with respect to Ca concentration and conductivity, but not with respect to depth of organics or degree of decomposition. This suggests an ionic (alkalinity-acidity) rather than hydrologic gradient, with the *Carex lasiocarpa*-*Cladium mariscoides* Type representing the 'poorer' type. This corresponds well with the observation that in the northeastern United States, *Carex lasiocarpa* occurs at sites ranging from poor to rich, whereas *Carex aquatilis* is restricted to minerotrophically rich sites. These results also suggest that with respect to Group I, different environmental gradients (hydrologic vs. minerotrophic) may be associated with vegetation variation at different levels of classification.

CONCLUSIONS

Calcareous fens of western New England and adjacent New York State are similar to rich peatland fens throughout North America with respect to species composition, water chemistry, and the influence of hydrologic and minerotrophic gradients on vegetation distribution. Future attempts to develop regional classifications of fens should more fully evaluate seepage and seasonally inundated types. In cases where hydrologic and ionic (alkalinity-acidity) gradients do not appear to explain observed variability in vegetation, factors such as nutrients, developmental history, response to disturbance, or biotic interactions may be significant.

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HARVARD FOREST

HARVARD UNIVERSITY

PETERSHAM, MASSACHUSETTS 01366